A TIME BUDGET OF THE MALE DICKCISSEL (SPIZA AMERICANA)

by 530

ROBERT LEIGH SCHARTZ

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A MASTER'S THESIS

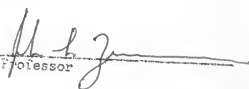submitted in partial fulfillment of the

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INTRODUCTION

Birds spend time performing a variety of activities during their annual and diurnal cycles. Each activity, depending on its duration and intensity, requires an expenditure of energy above the resting metabolic level. The environment influences the amount of time and energy necessary to perform various activities and, consequently, the survival and reproductive success of a bird. Theoretically, there is an optimum time and energy budget for a species, given a set of environmental conditions. Quantitative studies of various activities have been made by several investigators (Lees, 1948; Kluyver, 1950; Gibb, 1954, 1956 and 1960; Orians, 1961; Verbeek, 1964; Kale, 1965; Verner, 1965; Collias and Collias, 1967). Energy demands of activities as they occur in nature are more difficult to assess. LeFebvre (1964) determined the energy expenditure of pigeons in flight by using isotopically labeled water (D_2O^{18}). Rough estimates of the bioenergetics of breeding behavior have been given by Orians (1961) for certain blackbirds (Icteridae) and Kale (1965) for Long-billed Marsh Wrens (<u>Telmatodytes</u> <u>palustris</u>). Collias and Collias (1967) emphasized the need for the further development of physiological techniques that would make it possible to determine the energy requirements of birds in the field and suggested that oxygen consumption above the resting level be used as an index for comparisons of the energetics of various activities.

A necessary prerequisite to determining the energy budget and thus the energetic role of a species in its community is an analysis of the proportionality of the energy-demanding activities in the life of the bird. In this study, field data collected in Kansas were used to quantify the distribution of time among the various breeding activities of the male Dickcissel

(Spiza americana), often the only avian consumer species in the old field sere.

STUDY AREA

A tract of 65 acres in section 31, T8S, R6E, Riley County, Kansas, was used in this study (fig. 1) and is part of the 128-acre study area described by Zimmerman (1966). Twenty-seven percent of this ground was in wheat until harvested on 17 July 1967 when lambsquarters (Chenopodium album) became dominant. Extensive stands of kochia (Kochia scoparia), ragweed (Ambrosia trifida), sunflowers (Helianthus sp.), sweetclover (Melilotus alba and M. officinalis), horseweed (Conyza canadensis) and a variety of other annual forbs with patches of smooth brome (Bromis inermis) constituted 20 percent of the cover, mainly along a waterway extending the length of the study area. Mixed grasses (B. inermis, B. tectorum, Bouteloua curtipendula, Sporobolus clandestinus, Andropogon scoparius) covered 23 percent of the area, while the remaining 30 percent was dense smooth brome (B. inermis). A list of common plants identified on this plot in July 1966 is in the appendix (table 11).

Mean monthly temperatures, total monthly precipitation and mean vegetation heights calculated from data collected in the first week of July are given in table 1 for 1966 and 1967. The range of daytime temperatures is indicated by mean maximum and minimum temperatures. The method of vegetation analysis was described by Zimmerman (1966).

Relatively high daytime temperatures and low rainfall in May and June 1966 combined to drastically affect the vegetation. Grasses and short forbs, medium forbs, and tall forbs averaged 22, 45 and 97 cm less in 1966 than in 1967.

WHEAT

FORBS

MIXED GRASSES

BROME

0'   330'   660'
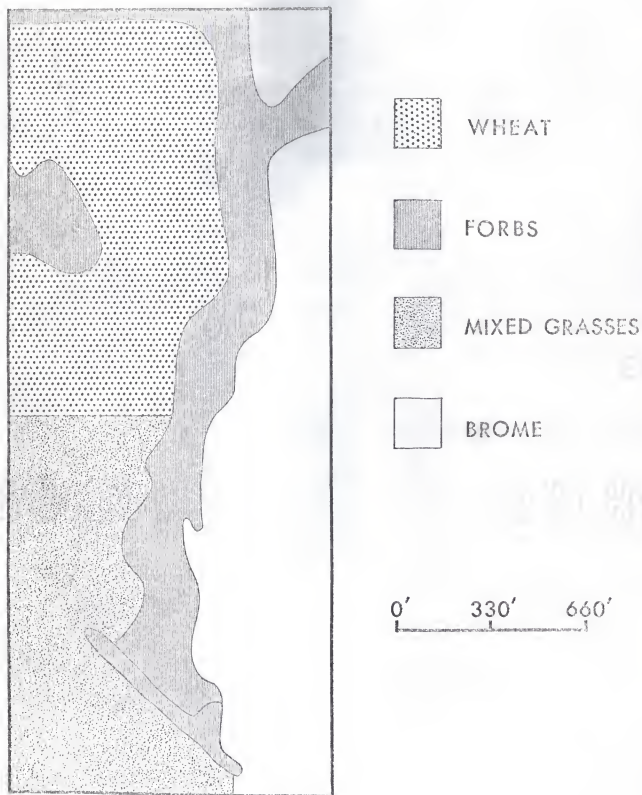
Fig. 1. Vegetation of the study area.

Table 1. Temperatures, precipitation and vegetation heights.

Month	Mean Maximum Temperature °F	Mean Minimum Temperature °F	Mean Ambient Temperature °F	Precipitation in inches	Mean Heights in cm, First Week in July		
					Grass and Short Forbs	Medium Forbs	Tall Forbs
1966							
May	78.0	52.0	65.0	1.87			
June	85.5	62.9	73.6	1.74			
July	96.1	72.3	85.0	2.36	29	55	75
August	85.5	63.6	75.1	4.44			
Total				10.41			
1967							
May	74.7	50.5	62.5	2.95			
June	83.0	62.4	73.0	5.25			
July	86.0	63.5	75.2	4.93	51	100	182
August	86.6	61.5	74.3	1.48			
Total				14.61			
1968							
May	71.0	49.6	62.5	2.51			

METHODS

Dickcissels were captured with mist nets, and combinations of colored leg bands were used to mark individual birds. Not all of the banded birds became residents on the study area. Only one male was unbanded and individual recognition was made on the basis of song and color pattern. In 1966, 17 Dickcissels (12 males and 5 females) were banded. Six of the males banded in 1965 returned in 1966. They represent a 50 percent return of the 12 banded males resident on the study area during the previous year. During 1967, 49 Dickcissels (28 males and 21 females) were banded. Eight males were previously banded (four in 1965 and four in 1966). Seven of these males represent a 58 percent return of the 12 banded males resident in 1966 (one male was resident in 1965 but not 1966). In 1968, seven males returned (one banded in 1965, three banded in 1966, three banded in 1967). Six of these males represent a 26 percent return of 23 banded males resident in 1967 (one male was resident in 1966 but not 1967). Only one female, banded in 1967 and recaptured in 1968, was known to have returned to the study area. Banding was continued throughout the breeding season in 1968 and 73 Dickcissels (48 males and 25 females) were captured.

Both in 1967 and 1968 a thermograph housed in a standard weather station provided a continuous record of temperature, while rainfall on the study area was measured with a 4-in. diameter rain gauge. Weather data for 1966 were obtained from Manhattan station No. 2 at Kansas State University located 20 miles east of the study area.

Samples of arthropod populations were taken on the four vegetation patches on eight days between 26 June and 17 July 1967. Two patches (mixed grasses and B. inermis) were included together so that the results show

arthropod numbers found in three areas (grasses, forbs, and wheat). Two methods of sampling were used. Forty-eight sweeps with an insect net were considered a sample of one square meter (Shelford, 1951). Samples were also taken with an aluminum box open at one end and measuring 31.6 x 31.6 x 77 cm. The open end of the box was pushed to the ground through the vegetation and an insecticide was sprayed through a lid on top to kill anything inside. All the vegetation was then removed from the box and examined, and the 0.1 m^2 area of ground searched for arthropods. Specimens collected were preserved and later identified. In a few areas forbs were too dense or tall for the box to be effective. Sample sites, evenly distributed over the study area, were selected and marked on a scale map prior to the field work. Only a crude estimate of the numbers and kinds of insects and other arthropods and their distribution in the three vegetation types could be discerned from this work.

The Dickcissel population was measured from census data collected over weekly periods. Territorial boundaries and locations of males were recorded on scale maps of the study area and calculations of territory size were made by tracing their outlines with a compensating polar planimeter. A constant record of the number of mates present on the territories was kept. Nearly all of the nests of females which had established pair bonds with males selected for this study were found and their locations and contents recorded.

Randomly selected male Dickcissels (10 in 1966, 13 in 1967 and 7 in 1968) were observed with binoculars and telescope. Their activities were timed with a stop watch and recorded in sequence on 17 days between 27 June and 18 July 1966, on 60 days between 2 June and 17 August 1967, and on 18 days between 14 May and 9 June 1968. Total observation time in this study

was 326.1 hours: 52.3 hours in 1966, 212.9 hours in 1967 and 60.9 hours in 1968. Observations were conducted over a period of six to nine hours, either in the morning beginning at 0500 or in the afternoon ending at approximately 1945. All references to time are in CST. Observations of each bird began on the hour and lasted for 45 minutes. This allowed time for moving to a new location before beginning observations on the next bird. In this paper, time budgets are expressed as percentages of the observation period but statisical treatments were performed on values expressed as minutes per hour. Only those data in 1967 (i.e., weeks 8, 9 and 10 of the reproductive cycle) which span the same time period as the 1966 data were used in comparisons made between these two years. The categorized activities of the males are discussed below.

ACTIVITIES OF MALES

Foraging.--This includes all the time spent acquiring food. Dickcissels flit through the lower vegetation in search of insects or seeds, and it was necessary to assume males were foraging when they could not be seen. This was a reasonable assumption since other activities are usually performed in conspicuous places and often involve vocalizations. Some birds spent much of their foraging time in the wheat field where they could be seen at times feeding on the grain. Occasionally a bird was seen with an insect in its beak or wiping its bill after returning from a trip to the vegetation. Time spent resting or preening may have been included in this category but was considered negligible since birds were rarely static, usually emerging from the vegetation some distance from their original point of entry.

Resting.--This includes time spent resting or preening. A bird was recorded resting if it was inactive or if it preened for more than 30 seconds.

Resting between songs was of such short duration that the time spent was included as singing.

Singing.--Short intervals between songs as well as the time used in vocalization are included in this activity. Singing functions in mate attraction, territory defense and may also be an epidiectic display enabling birds to assess population density (Wynne-Edwards, 1962).

Territory defense.--This includes time spent in defensive activities other than song, such as aggressive display, chasing and fighting. Boundary disputes usually began with a confrontation of two males and a display of black throat patches. Eventually this may have terminated in a sudden vertical flight and actual fighting but ordinarily one of the males retreated before fighting ensued. Vigorous pursuit of an intruding male by the territorial male was the most common expression of aggressive behavior.

Courtship.--The time from the female's first arrival on the territory to nest completion spanned almost a week. During this period sexual chasing and copulations were frequent and the male spent much time with the female, flying from perch to perch each time the female moved. Although attending the female, the male often sang from perches near the female and it was also common for the male and female to forage together. In these instances males were recorded singing or feeding although they were attending a female.

Maintenance of the female.--This includes time spent attending the female after the nest was constructed on the territory. The male continued his attentiveness during egg laying and incubation, exchanging "chipping" notes with the female or following her when she was off the nest. This behavior waned during the brooding phase.

Distant flight.--Male Dickcissels sometimes left their territories, usually flying out of sight but occasionally landing 200 or 300 yards from the territory.

Interspecific aggression.--Interspecific contests were infrequent and lasted only a few seconds. Nearly all encounters were with the Red-winged Blackbird (Agelaius phoeniceus) which was the only other nesting species sharing this habitat with the Dickcissel. Male Redwings contested Dickcissels for perch sites and female Redwings, protecting the area around their nests, sometimes chased male Dickcissels.

RESULTS

Time Budget During the Reproductive Cycle

The weekly averages of the percent time spent in eight activities are graphed in figure 2. The number of observations for each week (i.e., sample size) and the maximum weekly density of males on the study area are indicated at the top of the graph. The reproductive cycle in this latitude begins with the arrival of males in the first week of May. Females arrive in the next week and the height of nesting occurs in the seventh week (mid-June). Portions of the yearly reproductive periods were synchronous for 1966, 1967 and 1968 since the arrival of the males, the arrival of the females and first nest construction occurred within 3, 7 and 10 day intervals, respectively, for all three years. Table 2 gives the average percent of time spent in each activity for each year. Appendix tables 12, 13 and 14 give average time budgets of males and appendix tables 15, 16 and 17 show the number of observations begun at each hour for each male.

Foraging.--Foraging varied less than any other activity, averaging 17 to 21 percent of the time budget throughout the breeding season. A slight
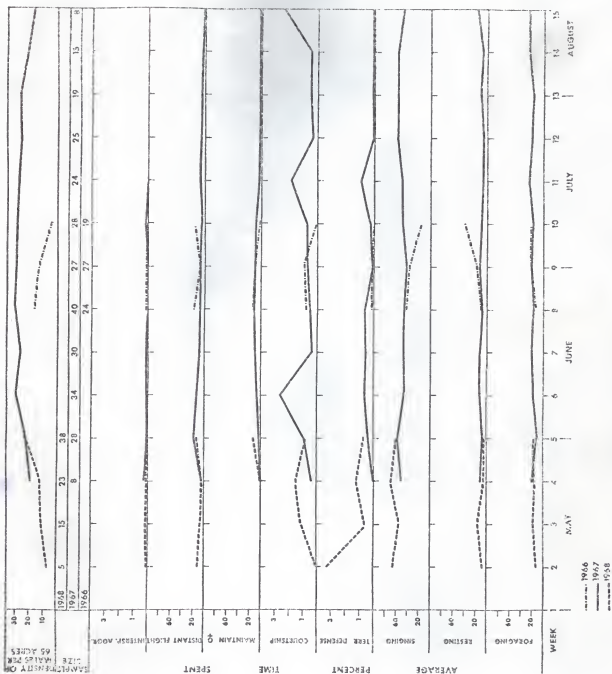
Fig. 2. Weekly averages of the percent time spent in eight activities, the number of observations for each week and the maximum weekly density of males on the study area.

Table 2. Average time budget of males expressed as percent time.

Year	Foraging	Resting	Singing	Territory Defense	Courtship	Maintain Female	Distant Flight	Intersp. Aggr.	Sample Size
1966	20.09	21.48	33.66	0.04	0.64	9.75	14.28	0.06	70
1967	19.80	10.40	50.78	0.43	0.97	7.85	9.75	0.02	286
1968	17.00	8.18	62.82	0.93	0.86	0.27	9.82	0.12	81

increase in August 1967 occurred at the onset of postnuptial molt. A similar increase was not evident at the beginning of postnuptial molt in 1966 (week 10), but males may have been foraging during distant flights.

Resting.--Except for a sharp increase in the first week of July 1966, resting was relatively stable at a level of 8 to 10 percent. Associated with the increase in resting in 1966, a reduction in the time budget took place for all other activities except distant flight which increased and foraging which remained unchanged.

Singing.--Singing was most intense early in the season at the time of territory establishment (week 2) and during the major influx of females (weeks 3 and 4), averaging 64.6, 55.0, 70.5 and 60.6 percent for weeks 2 through 5, respectively, in 1968. For the rest of the season singing comprised between 50 and 60 percent of the daily time budget. Song rates (songs per minute) taken during routine observations averaged 9.36 (S.E. = 0.233) in 1966, 10.11 (S.E. = 0.076) in 1967 and 8.94 (S.E. = 0.120) in 1968.

Territory defense.--During territory establishment in the second week, territory defense averaged 3.5 percent, decreasing to approximately one percent the third week and to nearly zero in the last four weeks.

Courtship.--Since there were no females until near the end of the second week, courtship was zero, gradually increasing with the arrival of females. In 1967 a peak occurred in the sixth week prior to the height of nesting in the seventh week. Two smaller peaks in the eleventh and fifteenth weeks are difficult to assess. They appear to be associated with the third and fourth cuttings of hay in adjacent agricultural land and might have been due to an influx of females resulting from nest failures due to mowing. Initial nest failures on the study area may also have contributed to an increase in the

number of courting females in the eleventh week. Courtship in week 15 led to copulations but nesting attempts were unsuccessful.

Maintenance of the female.--Time spent maintaining females began in the fourth week, reaching a maximum the eighth week as the number of incubating and brooding females increased. A decline in nesting activities beginning the eleventh week was paralleled by a decrease in maintenance of females.

Distant flight.--Distant flight was highest early in the breeding cycle, steadily decreasing after a maximum of 20 percent in the fifth week.

Interspecific aggression.--This activity accounts for a minor portion of the time budget and became nonexistent by the eleventh week in this study.

The maximum density of territorial males in 1966 was 18 compared to 30 in 1967. For the first five weeks densities of males in 1968 were similar to 1967 densities. The reduction of the number of males in July 1966 was related to an early cessation of reproduction.

Diurnal Activity Patterns

Diurnal activity patterns (fig. 3) were obtained by averaging percentages of time spent by all males in each activity for hourly intervals. The total hourly observations for each year were averaged together in this analysis with no adjustments made to account for differences in day length. The maximum variation in photoperiod was 19 minutes in 1966, 83 minutes in 1967 and 36 minutes in 1968. Disparity in 1966 and 1968 was not considered large enough to alter the results. Anticipating that changes in day length might affect the results of the 1967 data, percentages were averaged for two-week intervals as well as the total twelve weeks. There were no major differences in the diurnal activity patterns for the six biweekly intervals and diurnal patterns were as effectively demonstrated by averaging hourly
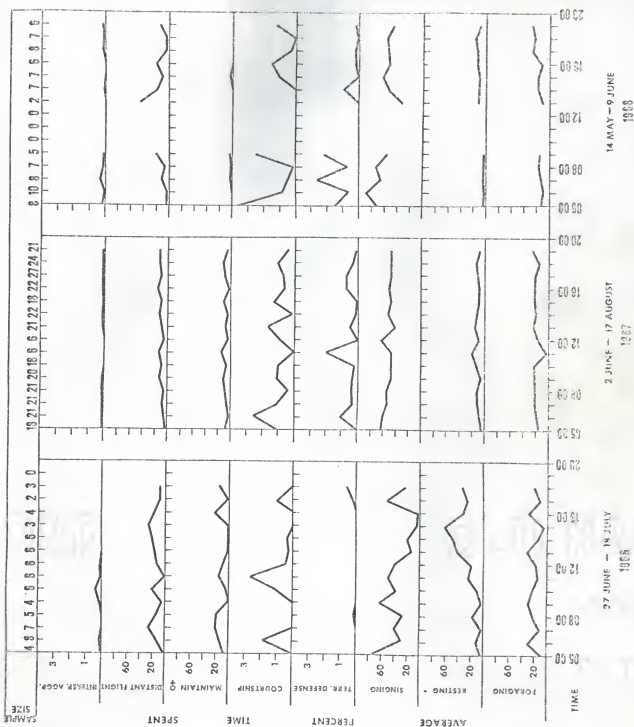
Fig. 3. Diurnal activity patterns for portions of the reproductive cycle
in 1966, 1967 and 1968.

observations for the total 12 weeks. The reduced variation in the 1967 graphs compared to the 1966 and 1968 graphs is due largely to greater sample size.

Foraging.--Birds commonly have bimodal daily feeding patterns even at moderate temperatures (Baldwin and Kendeigh, 1938). During the breeding season the male Dickcissel seems to lack such a predilection, as evidenced by the absence of diurnal changes in the feeding pattern in 1966 and 1967. In 1968 a gradual increasing trend was evident in the afternoons, indicating there may be some energy storage for nocturnal thermoregulator demands since May nights are still cool. The average minimum temperature was 47° F for 18 days from 14 to 31 May 1968.

Resting.--Resting was below average in the mornings of 1968 and more than doubled in the afternoons when singing, territory defense and courtship became less intense. Resting was nearly constant in 1967 but a substantial increase in the afternoons of 1966 corresponded inversely with reduced time spent singing.

Singing.--For all three years, singing was linearly dependent on time of day. The coefficients of dependence (slopes) of calculated regression lines were negative and significant (for 1966, $b = -1.72$, $t_b = -2.58$, d.f. = 13, $P < 0.025$; for 1967, $b = -0.50$, $t_b = -2.72$, d.f. = 14, $P < 0.01$; for 1968, $b = -1.24$, $t_b = -3.35$, d.f. = 11, $P < 0.005$). The highest averages for any activity were obtained for singing in 1968 at the initiation of the breeding cycle. The average of eight observations at 0500 was 74.4 percent and for 10 observations at 0600 was 88.9 percent. On one occasion at 0700 on 25 May 1968, a male sang constantly from the same perch for 45 minutes. Although decreasing with time, singing never dropped to a low level. Male Dickcissels sing constantly throughout the day.

Territory defense.--No diurnal pattern in territory defense was conspic-
uous in 1967 but in 1968 the greatest activity was in the mornings, decreas-
ing appreciably in the afternoons. Territory defense in 1966 was rarely
observed.

Courtship.--Courtship was also sporadic, lacking a diurnal pattern
except in 1968 when there was an early morning peak. Less time was spent
courting during the three-week period in 1966 than in the other two years.

Maintenance of the female.--This activity was relatively stable at a
level of 7 to 10 percent. Variation in 1966 was partly due to small sample
size. Low or zero averages in 1968 were consistent with the lack of nesting
females.

Distant flight.--Averages for distant flight in 1966 were higher than
in 1967 but no difference in the distribution of time spent was detected.
Time spent in distant flight for 1967 and 1968 increased slightly with time
of day.

Interspecific aggression.--Aggressive encounters, mainly with the Red-
wing Blackbird, were interspersed throughout the day. In 1966 no inter-
species contests were observed in the afternoons.

Territory Sizes

Territory sizes and the movement of the males within their territories
(i.e., the number of perch changes per hour) are given for 1966 in table 3
and for 1967 in table 4. Territories in 1966 were significantly larger than
territories in 1967 (t = 5.53, d.f. = 169, P < 0.0005). The means of ter-
ritory sizes of males in 1966 were not significantly different but a signif-
icant difference between the means of territory sizes was detected in 1967
(F = 13.12, d.f. = 10, 104, P < 0.0005). Differences in territory sizes in

Table 3. Territory size (mean acres ± S.E.) and activity in the territory (mean number of perch changes per hour ± S.E.) in 1966.

Male	Territory size	Sample size	Number of perch changes	Sample size
901	1.27 ± 0.153	9	10.5 ± 3.14	14
909	2.12 ± 0.257	6	19.8 ± 3.01	8
923	1.66 ± 0.078	8	9.8 ± 1.59	9
943	1.83 ± 0.241	7	15.9 ± 1.85	8
965	1.87 ± 0.173	7	19.0 ± 4.71	7
967	1.46 ± 0.227	5	17.0 ±14.00	2
973	1.78 ± 0.408	2	8.3 ± 2.03	3
974	2.06 ± 0.143	4	14.4 ± 3.06	5
975	2.22 ± 0.279	5	9.7 ± 2.65	6
981	1.68 ± 0.167	3	10.6 ± 1.80	8
Average	1.76 ± 0.070	56	13.2 ± 1.083	70

Table 4. Territory size (mean acres ± S.E.) and activity in the territory (mean number of perch changes per hour ± S.E.) in 1967.

Male	Territory size	Sample size	Number of perch changes	Sample size
501	1.07 ± 0.063	12	31.7 ± 2.61	22
507	1.35 ± 0.088	8	24.7 ± 2.61	24
510	0.97 ± 0.080	8	23.0 ± 2.19	22
513	0.93 ± 0.043	12	20.5 ± 2.11	26
532	0.98 ± 0.071	7	25.2 ± 2.76	21
533	1.19 ± 0.109	8	13.3 ± 1.34	23
535	1.47 ± 0.103	11	20.5 ± 2.01	20
901	0.87 ± 0.081	11	21.0 ± 1.54	32
923	1.03 ± 0.067	13	19.1 ± 1.65	30
931	1.63	1	23.0 ± 4.04	3
965	1.31 ± 0.047	13	43.4 ± 2.91	34
975	2.38 ± 0.293	12	28.4 ± 2.47	28
001	1.23 ± 0.041	8	38.0	1
Average	1.25 ± 0.015	124	25.2 ± 0.823	286

1967 were not attributable to time spent in any activity. Coefficients of linear correlation relating singing time to territory size and resting time to territory size were not significant. Zimmerman (1966) found that mated males had significantly larger territories than bachelor males. It follows, therefore, that territory sizes of mated males might vary with the number of mates. Means of territory sizes of mated males in 1967 were not significantly correlated with the mean number of mates (table 7) or to the total number of nests constructed on the territory (table 6). Males that were more active might have been expected to have larger territories but again the coefficient of linear correlation comparing the means of these two variables was not significant.

Although the vegetation data are not sufficient, there is evidence to support the hypothesis that territory size is inversely related to vegetational development. Environmental effects in 1966 reduced the percentage of cover and the height of the vegetation; therefore, the habitat was more homogeneous. Perhaps related to the homogeneity, territory sizes did not vary significantly between males and they were larger, compensating for reduced vegetation. Vegetational differences in 1967 were more pronounced and territory sizes were significantly different. Smaller territories in 1967 corresponded inversely to greater vegetational development.

Nesting Success and Mate Attraction

Nesting success.—Nesting success is given in table 5 for 1966 and in table 6 for 1967. Nearly all of the nests on the study area were found in 1966 and an estimated 50 percent of all nests in 1967 were discovered, including virtually all nests constructed on territories of males selected for this study.

Table 5. Nesting success in 1966.

Male	Total number nests found	Nests fledging young	Nests fledging cowbirds[1]	Nests fledging Dickcissels[1]	Cowbird parasitism	Nests failing and causes		
						Predation	Desertion[2]	Weather
901	1	0	0	0	0	1	0	0
909	1	1	1 (1)	0	0	0	0	0
923	3	0	0	0	0	2	1	0
943	1	0	0	0	0	1	0	0
965	2	0	0	0	0	0	2	0
967	1	0	0	0	1	0	0	0
973	1	0	0	0	0	1	0	0
974	1	1	1 (1)	0	0	1	0	0
975	2	0	0	0	0	0	0	0
981	1	0	0	0	0	1	0	0
003	1	0	0	0	0	1	0	0
Totals	15	2	2 (2)	0	2	8	3	0
Percent	100	13.3	13.3	0	13.3	53.3	20,1	0

[1] Numbers of young fledged are indicated in parentheses.
[2] Other than a result of cowbird parasitism.

Table 6. Nesting success in 1967.

Male	Total number nests found	Nests fledging young	Nests fledging cowbirds[1]	Nests fledging[1] Dickcissels	Nests failing and causes			
					Cowbird parasitism	Predation	Desertion[2]	Weather
501	5	0	0	0	0	5	0	0
507	3	0	0	0	0	3	0	0
510	3	1	0	1 (2)	0	2	0	0
513	3	1	1 (1)	1 (2)	2	0	0	0
522	2	0	0	0	0	1	0	0
533	1	0	0	0	0	1	1	0
535	1	0	0	0	0	1	0	0
901	2	0	0	0	0	1	1	0
923	5	0	0	0	0	5	0	0
931	0	0	0	0	0	0	0	0
939	2	0	0	0	1	1	0	0
965[3]	12	3	1 (1)	3 (6)	0	9	0	0
975	4	1	0	1 (2)	0	1	2	0
001	1	1	1 (2)	0	0	0	0	0
unbanded males	12	3	2 (3)	3 (5)	2	5	0	2
Totals	56	10	5 (7)	9 (17)	5	35	4	2
Percent	100	17.9	8.9	16.1	8.9	62.5	7.2	3.6

[1] Numbers of young fledged are indicated in parentheses.
[2] Other than a result of cowbird parasitism.
[3] Attempts to locate two nests on the territory of male 965 were unsuccessful.

One cowbird was fledged from each of the two nests fledging young in 1966. Nesting success was 13.3 percent for cowbirds and zero percent for Dickcissels in 1966, and 8.9 percent for cowbirds and 16.1 percent for Dickcissels in 1967. Predation accounted for 53.3 percent of the failures in 1966 and 62.5 percent of the failures in 1967. A large majority of nests were presumably pillaged by reptiles since they were found empty but not torn apart. Eggs were found missing from five nests in 1966 and 23 nests in 1967. In one instance a large bull snake (*Pituophis melanoleucus*) was seen ingesting three young Dickcissels about to fledge while both adults gave alarm notes nearby. The higher population of Dickcissels on the study area in 1967 was accompanied by a reduction in the number of nests deserted as a result of cowbird parasitism (13.3 percent in 1966 and 8.9 percent in 1967). Two nests in 1966 were abandoned upon completion of the nest and prior to egg laying. A third nest was abandoned as a result of an attempt to set a blind near it. Two nests were abandoned late in construction in 1967. One nest was abandoned in the fourth day of brooding and one of the two young Dickcissels present the previous day was found dead in the nest. Another nest was destroyed by mowing and two others were rained out during a storm.

Mate attraction.--The mean number of perch changes in 1967 (table 4) was significantly dependent upon the average number of mates (table 7) present on the territory during routine observations ($r = 0.87$, d.f. = 10, $P < 0.01$) as well as the total number of nests (table 6) constructed on the territory ($r = 0.86$, d.f. = 10, $P < 0.01$). Male 965 was extremely successful in attracting mates. The total number of nests constructed on this male's territory was 14 (two were not located). On 18 and 19 June 1967, there were seven females in various phases of the nesting cycle and an additional female was

Table 7. Average number of mates ± S.E. for males in 1967. [1]

Male	501	507	510	513	532	533	535	901	923	965	975
Mean number of mates	1.182	1.417	0.773	0.731	0.571	0.261	0.450	0.563	1.200	3.500	1.036
S.E.	0.214	0.199	0.160	0.152	0.130	0.129	0.153	0.109	0.222	0.327	0.166

[1] Computations were made by averaging the total number of nesting and courting females observed during routine observations.

being courted, bringing the total number of mates to eight during those two days. The average number of mates for male 965 during the 1967 study was 3.5. More active than any other male, male 965 constantly moved from place to place in the territory, courting and maintaining females.

Since there was no significant relationship between the average number of mates per male and the average time spent in singing by each male, other factors must determine the desirability of males' territories to females. The mean number of mates per male in 1966 was 0.84 (S.E. = 0.080) and is significantly different from the average of 1.37 (S.E. = 0.122) for the comparable three weeks in 1967 (t = 3.31, d.f. = 164, P < 0.0005). This difference, along with the lower male density in 1966 (fig. 2), is indicative of a lower habitat suitability that year (Fretwell and Lucas, 1969) and is possibly related to the more poorly developed vegetation (table 1).

Arthropod Populations

Table 8 gives the results of arthropod sampling in 1967 using the sweep method and appendix table 18 gives the sampling results using the box method. The number of arthropods according to family for both methods is given in appendix table 19.

DISCUSSION

Foraging

Except for more intense activity early in the breeding season at the time initial matings take place, there is no peak of work; territorial advertisement continues at a high level, regardless of the number of mates a male has acquired (e.g., male 965). Due to a constant turnover of females resulting from a high incidence of nest failure, reproductive activity is similarly

Table 8. The results of the sweep method for sampling arthropod populations on the study area.

Average Number of Individuals / M²

Order	Forbs (n = 22)			Grass (n = 14)			Wheat (n = 3)		
	adult	immature	total	adult	immature	total	adult	immature	total
Coleoptera	10.0	0.4	10.4	0.1	3.1	3.2	3.7	1.0	4.7
Collembola	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0
Diptera	25.1	0.0	25.1	11.7	0.0	11.7	2.4	0.0	2.4
Ephemeroptera	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Hemiptera	7.3	3.7	11.0	0.8	0.6	1.4	11.3	5.7	17.0
Homoptera	24.6	4.1	28.7	14.6	0.5	15.1	3.3	3.3	6.6
Hymenoptera	2.2	0.1	2.3	1.6	0.0	1.6	0.0	0.0	0.0
Lepidoptera	0.6	2.7	3.3	0.4	1.5	1.9	0.0	1.7	1.7
Neuroptera	0.6	0.3	0.9	0.0	0.1	0.1	0.3	0.3	0.6
Odonata	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Orthoptera	0.9	28.1	29.0	4.4	28.8	33.2	1.0	5.0	6.0
Psocoptera	0.0	0.0	0.0	0.1	0.0	0.1	11.0	5.0	11.0
Thysanura	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.1	0.1	0.1	0.0	0.1	0.0	0.0	0.0
Other Arthropods	7.0	0.0	7.0	4.4	0.0	4.4	5.0	0.0	5.0
Total Average / M²	78.3	39.7	118.0	38.3	34.7	73.0	38.0	17.0	55.0

continuous. Thus foraging does not change since energy demands paralleled the sustained level of activity characteristic of polygynous behavior. Even in situations where there are compensating decreases in some activities as other activities increase, foraging seldom varies. For instance, in 1966 decreased singing, courtship and maintenance of the female compensated for a sharp increase in resting while foraging changed little. A slightly lower foraging level early in the season may have been augmented by foraging in distant flight (see below).

At temperatures below 60° F, chemical regulation in homeothermy becomes more important than physical regulation in the Dickcissel (Zimmerman, 1965a). In this study temperatures were rarely lower than 60° F during June, July and August. Even on May nights temperatures below 60° F did not last more than several hours. The energy demands of thermoregulation, therefore, were also relatively constant throughout the reproductive cycle. Only in 1968 when minimum temperatures averaged less than 50° F was there an increase in foraging in the evenings. Male Dickcissels apparently store more than enough energy to survive the night since singing and courtship are greater in the morning while foraging shows no change throughout the day. Natural selection should favor males that are able to spend more time singing early in the day because involvement of females in courtship activities was observed more often at that time. Lack (1946) also found that pair formation in the European Robin (Erithacus rubecula) usually takes place in the morning and Verner (1965) observed instances of mate-seeking behavior by female Long-billed Marsh Wrens only in the morning. Long periods of time devoted to foraging in the early morning could mean the loss of a potential mate. Males also forage with the females, particularly during the courtship period,

thereby meeting their own energetic demands while at the same time maintaining the pair bond. This behavior is also prevalent with females that have established nests. Males accompanied females on 412 of 1,074 (48.6 percent) feeding trips in 1967. This is probably an underestimate since the female is secretive and easily missed. A male will usually adjust the boundaries or even relocate the territory to include areas utilized by the female. Male 501 in 1967 established a new territory in a wheat field 40 yards from his first location when a female he was courting built a nest there. The nest failed in the fifth day of incubation and this male immediately began courting another female on a new territory 100 yards from the original site.

Percentages of foraging time spent in forbs, grass and wheat, the number of trips and the average percent time per trip are included in table 9. In all three years the amount of foraging in the habitat patches corresponded with the abundance of arthropods (table 8). Male Dickcissels spend the most time feeding in forbs where insects are most abundant. Lesser amounts of feeding in the grass corresponded with 38 percent fewer insects found there than in the forbs, while the least time spent foraging was in the wheat where insects were 53 percent fewer than in the forbs. Males fed extensively on grasshoppers which were present in large numbers in the forbs and grass. Utilization of the grasshopper population in the grass may be limited by the lack of available perches. The size of the grasshopper renders it a more efficient food item than most other insects. Foraging time in the wheat was spent feeding on the grain rather than on insects and trips to the wheat were longer since it takes more time to extract and eat the grain than to catch an insect. Dickcissels apparently like to feed on the succulent immature seed rather than the hardened mature seed. Because the grain was

Table 9. Percent of foraging time spent in each of three patches, number of trips and average percent time per trip.

Year	Forbs			Grass			Wheat		
	% Time spent	Number of trips	Average time per trip	% Time spent	Number of trips	Average time per trip	% Time spent	Number of trips	Average time per trip
1966	73.09	108	0.676	24.85	53	0.467	2.15	5	0.430
1967	67.88	728	0.093	17.74	176	0.101	14.38	170	0.846
1968	48.39	149	0.324	41.71	115	0.363	9.99	19	0.525

nearly mature at the time the study began in 1966, records of foraging in the wheat were scant while in 1968 observations were too early. The 1967 study, however, included the period when the seeds were immature, hence a substantially larger proportion of foraging time spent in the wheat that year.

Resting and Environmental Temperature

The linear correlation coefficient relating time of day to the average time spent resting in 1966 was positive and significant ($r = 0.76$, $d.f. = 13$, $P < 0.01$). Such a relationship was not detected in the 1967 data. However, in 1967 temperatures never exceeded 94° F during any of the observations while in 1966 temperatures exceeded 94° F during 23 observation periods and during 16 of these 23 observations temperatures were above 100° F! The mean time spent resting in 1967 was 6.25 minutes per hour ($S.E. = 0.225$) and for temperatures less than 95° F in 1966 resting averaged 6.13 minutes per hour ($S.E. = 2.019$). Combining these data for both years, resting averaged 6.23 minutes per hour ($S.E. = 0.252$) for temperatures less than 95° F.

Resting data obtained during observations when the temperature was greater than 94° F were analyzed separately yielding a multiple regression:

$$y = 1820.02 + (-18.49)T + (-58.42)H + (0.60)T \cdot H$$

where y = resting (minutes per hour), T = temperature, H = relative humidity, and $T \cdot H$ = the interaction of temperature and relative humidity. This analysis was necessary in order to account for the independent effects of temperature and humidity as well as their combined effect. At environmental temperatures exceeding the Dickcissel body temperature, heat is absorbed by the bird rather than lost. Heat loss by evaporative cooling of the breathing tract through panting becomes less effective at higher humidities. An interaction term is

included in the model because the effect of temperature is also dependent on the relative humidity.

The multiple correlation coefficient was significant (R = 0.70, d.f. = 22, P < 0.01). Three multiple regression lines are plotted in figure 4 using the average relative humidity (38 percent) and the relative humidities two standard deviations from the mean (35 and 41 percent). Data points are included for temperatures greater than 94° F. The horizontal line represents the average time spent resting for temperatures below 95° F.

The results of the multiple regression show that for temperatures greater than 94° F resting increases and increases at a greater rate as the relative humidity increases. At temperatures below 95° F the effect of relative humidity is probably very slight within the range of 35 and 41 percent. Zimmerman (1965a) determined a single thermal neutral point at 97° F. At environmental temperatures below this value existence energy increases with the increasing need for thermogenesis while at temperatures above this point existence energy increases due to metabolic demands of increased ventilation rates. It is quite evident from figure 4 that there is a compensating increase in resting when the bird is under physiological heat stress.

Table 10 compares the mean time spent in the various activities in 1966 with comparable means calculated from the 1967 data. Average song rates and perch changes are included because they give an indication of the level of activity. Interspecific aggression was not included since it comprises a minor portion of the time budget. The results show no significant difference between the two years for time spent in foraging, courtship and maintenance of the female. Resting was significantly higher in 1966 and males changed
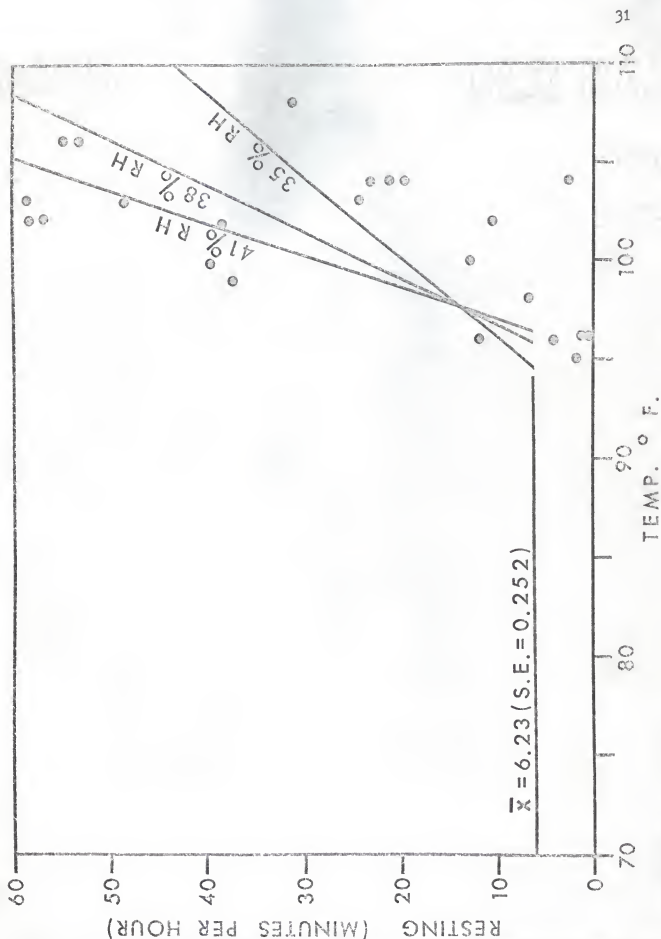
Fig. 4. Effects of environmental temperature and relative humidity on resting.

Table 10. Comparison of means (minutes per hour) of activities during weeks 8, 9 and 10 of the breeding cycle in 1966 and 1967 using the t test.

Activity [1]	Time spent (mean minutes per hour ± S.E.)		t values	Degrees of freedom	Probability
	1966	1967			
Foraging	12.06 ± 1.397	11.79 ± 0.849	0.170	164	P > 0.05
Resting	12.89 ± 2.061	6.27 ± 0.686	3.411	164	P < 0.0005
Singing	20.20 ± 2.132	27.91 ± 1.513	3.036	164	P < 0.005
Song rate (songs/minute)	9.40 ± 0.234	9.86 ± 0.139	1.780	228	P < 0.05
Territory defense	0.02 ± 0.017	0.24 ± 0.069	2.698	164	P < 0.005
Courtship	0.39 ± 0.193	0.37 ± 0.087	0.094	164	P > 0.05
Maintain female	5.85 ± 1.471	8.38 ± 1.481	1.184	164	P > 0.05
Distant flight	8.57 ± 1.811	5.12 ± 0.896	1.840	164	P < 0.05
Perch changes (perches/hour)	13.20 ± 1.083	22.85 ± 1.120	6.200	164	P < 0.0005

[1] Interspecies aggression was not included since it involves a minor part of the time budget, while song rate and perch changes are included because they give an indication of the level of activity.

perches significantly less often. Singing and territory defense were, on the other hand, significantly lower. In addition to the decreased singing, song rates were significantly lower in 1966. Thus the increase in resting necessitated by the high temperatures in 1966, particularly in July (table 1), produced a compensatory decrease in singing and territory defense. It is suggested that the early termination of the reproductive activity of the males by mid-July of 1966 is a direct result of this compensatory shift in the time budget of the males leading to decreases in singing and then courtship and maintenance of the female (fig. 2). The higher level of distant flight in 1966 may have resulted from increased time away from the territory in search of water due to an increase in the water requirements of the birds under heat stress (Zimmerman, 1965b). Water requirements of territorial Dickcissels seem to be normally satisfied by their food and the morning dew since open water is seldom available on a territory.

Distant Flight

Kluyver and Tinbergen (1953) in their studies of titmice (Paridae) were first to suggest that territorial behavior of resident birds is used as a density cue by unsettled birds so that they can avoid highly populated habitats. Similarly, Wynne-Edwards (1962) argued that singing is an epidiectic display in territorial birds. It was observed that male Dickcissels, even though they have established territories, periodically leave their territories (distant flight). It is hypothesized that this behavior allows males to assess the population density and habitat suitability in other locations. According to the hypothesis, a male would re-establish a territory in a new location providing the desirability of the new location exceeded the desirability of the male's original location. Males with more suitable habitats

would not be expected to spend as much time in distant flight as males with less suitable habitats because of the lower probability of finding a more suitable area. Because the Dickcissel is polygynous and all females have a free choice of mates, there is a selective advantage for females to select males with the most suitable habitats. Zimmerman (1966) found that the vegetation in territories of bachelor males was restricted in both height and percent of cover compared to vegetation in the territories of mated males. It follows that males with more mates will have higher habitat suitabilities. As a result, distant flight will be dependent on the number of mates, an index of the suitability of the habitat a male occupies.

The data collected during 286 routine observations in 1967 were analyzed according to the principles of multiple regression with three independent variables in order to correct for diurnal and day to day changes in distant flight. The hypothesis was made that distant flight was proportional to the number of mates, the time of day and the day of the reproductive cycle. The model is:

$$y = b_0 + b_1x_1 + b_2x_2 + b_3x_3$$

where y = distant flight in minutes per hour, x_1 = the number of mates (i.e., nesting and/or courting), x_2 = day of the reproductive cycle with day 1 beginning on 1 May 1967, and x_3 = hour of the day beginning with 0500 and ending with 1900.

In the results of the analysis the number of mates showed a significant negative relation to the time spent in distant flight ($b_1 = -1.16$, $t_{b_1} = -3.15$, d.f. = 282, $P < 0.005$). Day of the breeding cycle showed a significant negative relation to distant flight ($b_2 = -0.11$, $t_{b_2} = -4.44$, d.f. = 282, $P < 0.0005$) and time of day a significant positive relation to distant

flight (b_3 = 0.34, t_{b_3} = 3.18, d.f. = 282, F < 0.005). The multiple correlation coefficient was significant (R = 0.33, d.f. = 285, P < 0.01).

Figure 5 plots multiple regression lines using the coefficients of proportionality calculated from the data. The center line is a plot of an average day and hour (i.e., day 66 and hour 1200). The two dashed lines are plots using the average day as a constant and varying the time, using 0500 and 1900. These plots indicate that during an average day distant flight increased by nearly five minutes in the 14 hours between 0500 and 1900. The outermost solid lines are plots using the average hour (1200) but varying the day by two standard deviations (day 30 and day 102). These plots indicate that distant flight on the average decreased eight minutes in 72 days between 30 May and 10 August. Furthermore, for any given day and time, distant flight decreased with an increase in the number of mates.

The relationship between distant flight and number of mates and also the fact that this behavior is higher early in the nesting season supports the hypothesis that distant flight is a density assessment mechanism. Orians (1961) observed that colonies of Tricolored Blackbirds (A. tricolor) assess the food supply of the surrounding environment by means of mass feeding flights. In this study a significant inverse relationship between the mean time foraging and the mean time spent in distant flight was determined in 1967 (r = -0.88, d.f. = 10, P < 0.01). This is consistent with the hypothesis since foraging behavior may be used to assess the desirability of a habitat. The idea that males may move their territories to areas that are more suitable is plausible by virtue of the fact that it is not uncommon for males to disappear from their territories early in the breeding season.
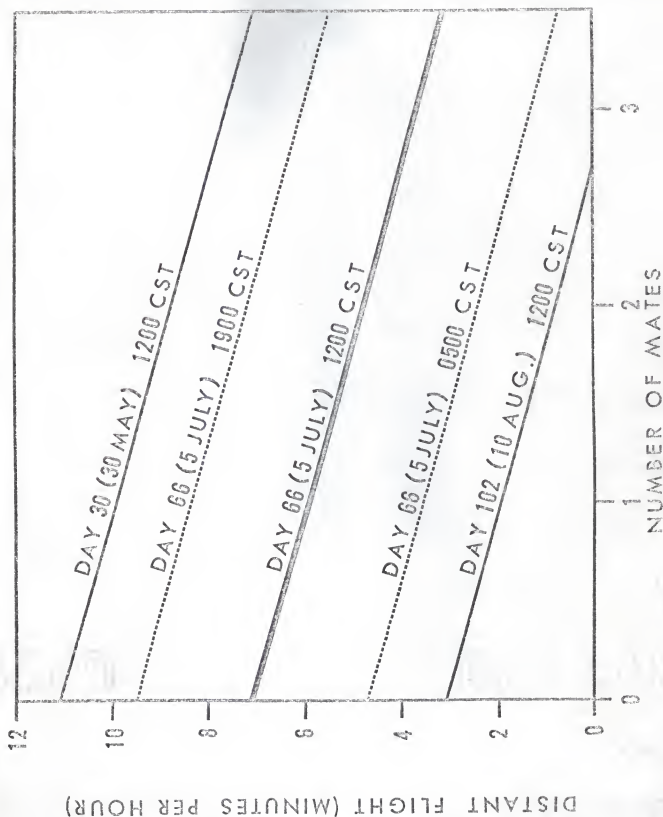
Fig. 5. Time spent in distant flight in relation to the number of mates, time of day, and day of the reproductive cycle.

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SUMMARY

The categorized activities of color-banded male Dickcissels were timed and recorded on 17 days between 27 June and 18 July 1966, on 60 days between 2 June and 17 August 1967, and on 18 days between 14 May and 9 June 1968. An average time budget, compiled from 326 hours of field observations, was constructed for the diurnal and reproductive cycles.

Foraging varied less than any other activity, changing little from day to day and lacking a typical bimodal diurnal pattern. This was explained on the basis that energy demands paralleled the sustained level of activity

characteristic of polygynous behavior and that energy demands of thermoregulation were relatively constant since temperatures were seldom below 60° F. An increasing trend in the evenings of 1968 may have been a result of a need for energy storage due to nocturnal thermoregulator demands since May nights are cool. Males foraged with females particularly during the courtship period, enabling them to meet their own energy demands while maintaining the pair bond. Most of the foraging time was spent in forbs where insects were most abundant.

Early in the breeding season resting increased slightly in the afternoons when reproductive activity was less intense. High levels of resting in the afternoons of 1966 corresponded inversely with reduced time spent singing. For temperatures greater than 94° F in 1966 resting increased and increased at a greater rate with increases in relative humidity. It was suggested that a significantly higher level of resting due to physiological heat stress led to early cessation of breeding activities in 1966 due to a compensatory shift in the time budget through a decrease in singing, courtship and maintenance of the female. Temperatures in 1967 did not exceed 94° F and resting did not change.

Singing was highest early in the breeding season at the time of territory establishment and in the mornings when courtship activities were more frequent. Male Dickcissels sing constantly throughout the day and singing normally averaged at least 50 percent of the time budget.

Territory defense was highest at the time of territory establishment. In 1966 territory defense was rarely observed; in 1967 no diurnal pattern was evident; but in 1968 a peak in territory defense occurred in the mornings.

Courtship gradually increased with the arrival of females and a peak

occurred in the week prior to the height of nesting. Initial nest failures on the study area and nest failures due to cuttings of hay may have resulted in additional courtship peaks in the eleventh and fifteenth weeks. Although copulations were observed as late as August 1967, nest attempts at that time were unsuccessful.

Maintenance of the female during the reproductive season corresponded with the nesting activity and no diurnal pattern was evident.

The Red-winged Blackbird is the only nesting species that shares the habitat with the Dickcissel and aggressive encounters between them were seldom observed.

The disappearance of males early in the breeding season may be an indication that they re-establish territories in other locations where the habitat is more desirable. It was hypothesized that in 1967 male Dickcissels left their territories (distant flight) to assess the population density and habitat suitability in other locations. Singing was suggested to be an epideictic display used as a cue by the birds to assess population densities. In a multiple regression analysis the number of mates was assumed to be an index of the suitability of the habitat a male occupies. The results were significant and showed that for fewer mates (a lower habitat suitability) distant flight increases. Distant flight decreased from day to day and increased with time of day. A significant inverse correlation between the mean time spent foraging and the mean time spent in distant flight was consistent with the hypothesis since foraging behavior may be used to assess the desirability of a habitat. In 1966 increased water requirements may have resulted in a higher incidence of distant flight since open water is rarely available on the territory.

Means of territory sizes of males in 1967 were not significantly correlated with the mean number of mates or the total number of nests constructed on the territory. Territory sizes of males in 1966 were not significantly different. Differences in territory sizes in 1967 were not attributable to time spent in any activity but rather it was suggested that territory sizes are related to vegetation development.

Resulting from high temperatures and low rainfall, grasses and short forbs, medium forbs, and tall forbs averaged 22, 45, and 97 cm less in 1966 than in 1967. A lower density of males and fewer mates per male was indicative of a lower habitat suitability in 1966 as compared to 1967. The level of activity of the males was positively correlated with the number of mates present on the territory and no significant correlation was detected between the average number of mates per male and time spent singing. Male 965 was extremely successful in attracting mates and at one time had established pair bonds with eight females. The total number of nests constructed on this male's territory was 14.

Sixty percent of all nests failed as a result of predation. Nesting success for Dickcissels was zero percent in 1966 and 16 percent in 1967.

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APPENDIX

Table 11a. Plants identified on the study area in July 1966. [1]

Family	Scientific Name	Common Name
Aceraceae	Acer negundo	box elder
Amaranthaceae	Amaranthus hybridus	tumbleweed
Asclepiadaceae	Asclepias speciosa Asclepias tuberosa	showy milkweed butterfly milkweed
Brassicaceae	Brassica juncea	indian mustard
Caprifoliaceae	Sambucus canadensis Symphoricarpos orbiculatus	American elderberry coralberry or buckbrush
Chenopodiaceae	Chenopodium album Kochia scoparia	lambsquarters kochia or summer cypress
Compositae	Ambrosia artemisiifolia Ambrosia psilostachya Ambrosia trifida Artemisia ludoviciana var. ludoviciana Cirsium altissimum Cirsium undulatum var. undulatum Conyza canadensis Helianthus annuus Helianthus maxmilliani Helianthus petiolaris Lactuca serriola Silphium integrifolium var. laeve Solidago altissima Solidago gymnospermoides Tragopogon dubius Vernonia baldwinii	common ragweed western ragweed giant ragweed Louisiana sagewort tall thistle wavyleaf thistle horseweed common sunflower maximillian sunflower prairie sunflower wild lettuce rosinweed goldenrod sticky goldenrod goatsbeard baldwin ironweed
Convolvulaceae	Convolvulus arvensis Ipomoea hederacea	field bindweed blue morning glory
Euphorbiaceae	Euphorbia maculata Euphorbia marginata	spotted spurge snow-on-the-mountain
Juglandaceae	Juglans nigra	black walnut
Juncaceae	Juncus interior	inland rush
Lamiaceae	Salvia azurea var. grandiflora Teucrium canadense var. virginicum	pitchers sage germander or wood sage

Table 11b.

Family	Scientific Name	Common Name
Leguminoseae	Glycyrrhiza lepidota Lespedeza capitata Melilotus alba Melilotus officinalis Psoralia tenuifolia var. floribunda	wild licorice roundheaded lespedeza white sweetclover yellow sweetclover common breadroot
Malvaceae	Abutilon theophrasti Hibiscus trionum	velvetleaf flower-of-an-hour
Moraceae	Maclura pomifera Morus alba Morus rubra	osage orange white mulberry red mulberry
Nyctaginaceae	Mirabalis nyctaginea	narrow leaf four-o-clock
Oenotheraceae	Oenothera biennis Oenothera laciniata var. laciniata	common evening primrose cutleaf evening primrose
Phytolacaceae	Phytolaca americana	common pokeberry
Poaceae	Andropogon gerardi Andropogon scoparius Bouteloua curtipendula Bromus inermis Bromus tectorum Panicum virgatum Sporobolus clandestinus	big bluestem little bluestem sideoats grama smooth brome downy brome switchgrass dropseed
Salicaceae	Populus sargentii	plains cottonwood
Solanaceae	Physalis virginiana Solanum carolinense Solanum rostratum	waterfall or ground cherry Carolina horsenettle buffalo bur
Ulmaceae	Ulmus americana	American elm
Umbelliferae	Conium maculatum	poison hemlock
Verbenaceae	Verbena stricta	wooly verbena

[1] T. M. Barkley, A Manual of the Flowering Plants of Kansas, 1968.

Table 12. Average time budgets of individual males in 1966 expressed as percent time.

Male	Foraging	Resting	Singing	Territory Defense	Courtship	Maintain Female	Distant Flight	Intersp. Aggr.	Sample Size
901	22.29	27.10	26.61	0.06	0.12	3.55	20.27	0.00	14
909	21.41	18.55	7.83	0.00	0.81	42.23	9.17	0.00	8
923	18.62	11.76	47.76	. . .	1.82	2.47	17.57	0.00	9
943	28.53	7.67	39.49	0.24	0.23	4.57	18.79	0.48	8
965	24.18	16.41	48.69	0.00	2.55	2.56	5.61	0.00	7
967	20.65	15.41	21.00	0.00	0.00	3.88	38.82	0.24	2
973	1.04	7.92	41.14	0.00	0.00	9.37	40.53	0.00	3
974	21.55	11.73	35.33	0.00	0.00	14.34	17.05	0.00	5
975	6.92	51.73	33.30	0.00	0.00	6.40	1.65	0.00	6
981	20.55	33.74	36.58	0.00	0.12	9.01	0.00	0.00	8
Average	20.09	21.48	33.66	0.04	0.64	9.75	14.28	0.06	70

Table 13. Average time budgets of individual males in 1967 expressed as percent time.

Male	Foraging	Resting	Singing	Territory Defense	Courtship	Maintain Female	Distant Flight	Intersp. Aggr.	Sample Size
501	23.01	8.00	58.78	0.80	1.46	3.15	4.71	0.09	22
507	10.62	6.38	53.66	0.12	2.01	9.89	17.31	0.01	24
510	23.56	1.25	66.07	0.12	0.84	1.64	6.52	0.00	22
513	15.02	18.85	26.74	0.03	1.15	24.71	13.50	0.00	26
532	20.54	10.59	47.09	1.33	0.40	4.56	15.45	0.04	21
533	9.81	12.06	54.69	0.03	1.68	2.28	19.44	0.01	23
535	21.87	6.88	64.03	0.21	1.24	1.08	4.67	0.02	20
901	23.77	7.66	58.25	0.78	0.38	2.19	6.97	0.00	32
923	24.01	17.23	44.36	0.27	0.13	6.54	7.45	0.01	30
931	24.55	11.45	43.14	0.00	0.00	0.00	20.86	0.00	3
965	22.83	10.20	45.78	0.72	1.25	15.21	3.98	0.03	34
975	22.27	12.03	47.85	0.12	0.73	7.88	9.11	0.01	28
001	31.60	11.80	29.50	0.00	0.00	15.90	11.20	0.00	1
Average	19.80	10.40	50.78	0.43	0.97	7.85	9.75	0.02	286

Table 14. Average time budgets of individual males in 1968 expressed as percent time.

Male	Foraging	Resting	Singing	Territory Defense	Courtship	Maintain Female	Distant Flight	Intersp. Aggr.	Sample Size
501	19.87	12.86	57.86	1.00	0.66	0.00	7.67	0.08	12
513	15.76	7.42	65.62	0.65	0.25	0.41	9.70	0.19	24
525	10.10	6.95	74.76	2.74	0.83	1.07	3.41	0.14	7
931	21.62	3.24	50.57	1.14	1.34	0.35	21.53	0.21	13
965	12.68	6.05	71.39	0.75	3.68	0.00	5.45	0.00	7
981	18.46	11.41	62.62	0.26	0.39	0.00	6.86	0.00	17
004	6.15	3.63	74.30	4.20	0.00	0.00	11.60	0.12	1
Average	17.00	8.18	62.82	0.93	0.86	0.27	9.82	0.12	81

Table 15. Number of observations beginning at each hour for males in 1966.

Male	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	Total
901	0	0	3	1	0	0	1	2	1	2	2	1	1	0	0	14
909	2	3	0	1	0	1	1	0	0	0	1	1	0	0	0	8
923	0	0	1	1	2	1	1	0	1	0	0	0	0	0	0	9
943	0	1	0	0	1	2	0	1	0	1	0	1	0	1	0	8
965	0	2	0	1	0	1	0	0	2	0	0	0	1	0	0	7
967	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
973	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	3
974	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	5
975	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	6
981	1	1	0	1	0	0	2	2	0	1	0	0	0	0	0	8
Total	6	7	7	5	4	6	6	6	6	6	3	4	2	2	0	70

Time (CST)

Table 16. Number of observations beginning at each hour for males in 1967.

Male	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	Total
501	0	1	2	4	1	1	0	0	1	1	2	2	5	1	1	22
507	1	3	2	1	1	4	2	2	1	1	2	2	1	0	1	24
510	4	2	1	1	2	2	0	1	2	0	3	0	2	0	2	22
513	1	2	2	1	1	4	0	0	1	1	2	2	3	4	2	26
532	0	1	3	1	1	2	2	0	2	2	1	3	2	1	0	21
533	3	2	0	0	2	2	1	0	4	2	1	1	0	3	2	23
535	3	1	2	1	0	0	1	2	0	1	2	0	2	2	3	20
901	1	3	3	1	2	0	0	1	1	5	1	5	1	4	4	32
923	0	0	2	3	5	1	0	0	2	3	3	3	5	3	0	30
931	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	3
965	2	2	1	3	5	2	0	0	5	2	0	2	4	4	2	34
975	3	4	2	4	0	0	0	0	2	3	1	1	2	2	4	28
001	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Total	18	21	21	21	20	18	6	6	21	22	18	22	27	24	21	286

Time (CST)

Table 17. Number of observations beginning at each hour for males in 1968.

Male	Time (CST)															Total
	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	
501	1	2	1	2	1	0	0	0	0	0	1	1	2	0	1	12
513	2	3	2	0	1	0	0	0	1	4	2	2	3	4	0	24
525	1	0	1	0	2	0	0	0	0	0	1	0	1	0	1	7
931	1	1	3	1	0	0	0	0	0	1	0	2	0	1	3	13
965	1	2	0	0	1	0	0	0	0	0	2	1	0	0	0	7
981	2	2	1	4	0	0	0	0	1	1	1	0	2	2	1	17
004	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Total	8	10	8	7	5	0	0	0	2	7	7	6	8	7	6	81

Table 18. The results of the box method for sampling arthropod populations on the study area.

Order	Average Number of Individuals / 0.1 M²								
	Forbs (n = 2)			Grass (n = 7)			Wheat (n = 15)		
	adult	immature	total	adult	immature	total	adult	immature	total
Coleoptera	0.5	0.5	1.0	0.3	0.0	0.3	2.2	0.9	3.1
Collembola	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2
Diptera	1.0	0.0	1.0	0.3	0.0	0.3	0.2	0.0	0.2
Ephemeroptera	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0
Hemiptera	0.5	0.0	0.5	0.0	0.1	0.1	3.3	6.0	9.3
Homoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.2	1.8
Hymenoptera	0.5	0.0	0.5	0.3	0.0	0.3	0.2	0.0	0.2
Lepidoptera	0.0	2.0	2.0	0.1	0.4	0.5	0.0	0.3	0.3
Neuroptera	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.5	0.5
Odonata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orthoptera	0.0	0.5	0.5	0.1	3.2	3.3	0.0	0.1	0.1
Psocoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2
Thysanura	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Arthropods	0.5	0.0	0.5	1.8	0.0	1.8	1.1	0.1	1.2
Total Average / 0.1 M²	3.0	3.0	6.0	3.1	3.7	6.8	7.9	9.2	17.1

Table 19a. The results of two methods of sampling arthropod populations on the study area.

Number of Individuals.[1]

Order / Family	Sweep Forbs A	I	T	Sweep Grass A	I	T	Sweep Wheat A	I	T	Box Forbs A	I	T	Box Grass A	I	T	Box Wheat A	I	T
Coleoptera																		
Anthicidae	220	9	229	1	43	44	11	3	14	1	1	2	2	0	2	32	13	45
Cantharidae	0	0	0	0	2	2	1	0	1	0	0	0	0	0	0	3	0	3
Carabidae	2	0	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Cerambycidae	2	0	2	1	0	1	0	0	0	0	0	0	1	0	1	4	0	4
Chrysomelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cicindellidae	104	3	107	0	13	13	1	0	1	0	0	0	1	0	1	4	0	4
Cleridae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coccinellidae	6	0	6	0	1	1	2	0	2	1	0	1	0	0	0	0	0	0
Curculionidae	6	0	6	0	2	2	1	1	2	0	1	1	0	0	0	2	2	4
Dermestidae	6	6	12	0	14	14	2	0	2	0	0	0	0	0	0	0	0	0
Elateridae	66	0	66	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Histeridae	7	0	7	0	1	1	0	0	0	0	0	0	0	0	0	8	0	8
Hydrophilidae	2	0	2	0	4	4	0	0	0	0	0	0	0	0	0	1	0	1
Lampyridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathridiidae	11	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malachiidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Meloidae	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1
Phalacridae	2	0	2	0	1	1	4	0	4	0	0	0	0	0	0	0	0	0
Scarabaeidae	7	0	7	0	0	0	0	1	1	0	0	0	0	0	0	1	1	2
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenebrionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
misc.	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	10	0	10
Collembola																		
Sminthuridae	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	3	0	3

Table 19b.

Order / Family	Number of Individuals																	
	Sweep Method									Box Method								
	Forbs			Grass			Wheat			Forbs			Grass			Wheat		
	A	I	T	A	I	T	A	I	T	A	I	T	A	I	T	A	I	T
Diptera	553	0	553	164	0	164	7	0	7	2	0	2	2	0	2	4	0	4
Agromyzidae	22	0	22	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Anthomyiidae	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asilidae	8	0	8	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Bombyliidae	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cecidomyiidae	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae	2	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae	7	0	7	8	0	8	0	0	0	0	0	0	0	0	0	0	0	0
Chloropidae	40	0	40	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Conopidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Culicidae	23	0	23	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Dolichopodidae	45	0	45	10	0	10	0	0	0	2	0	2	2	0	2	2	0	2
Drosophilidae	6	0	6	2	0	2	1	0	1	0	0	0	0	0	0	0	0	0
Empididae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae	336	0	336	122	0	122	4	0	4	0	0	0	0	0	0	0	0	0
Piophilidae	0	0	0	2	0	2	1	0	1	0	0	0	0	0	0	0	0	0
Pipunculidae	4	0	4	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Sarcophagidae	3	0	3	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Scatopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Sciaridae	7	0	7	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Sciomyzidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepsidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syrphidae	29	0	29	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tachinidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tephritidae	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Therevidae	1	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
misc.	4	0	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 19c.

Order / Family	Sweep Method — Forbs A	I	T	Sweep Method — Grass A	I	T	Sweep Method — Wheat A	I	T	Box Method — Forbs A	I	T	Box Method — Grass A	I	T	Box Method — Wheat A	I	T
Ephemeroptera																		
Baetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	90	139
Ephemeridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	84	121
Hemiptera	161	81	242	12	8	20	34	17	51	1	0	1	0	0	0	10	0	10
Coreidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corizidae	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cydnidae	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Lygaeidae	10	2	12	6	1	7	8	6	14	0	0	0	0	0	0	0	0	0
Miridae	137	66	203	6	2	8	15	3	18	0	0	0	0	0	0	10	0	10
Nabidae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pentatomidae	3	2	5	0	3	3	0	1	1	0	0	0	0	0	0	0	0	0
Reduviidae	7	4	11	0	1	1	11	7	18	0	0	0	0	0	0	0	0	0
misc.	0	5	5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Homoptera	540	90	630	204	8	212	10	10	20	0	0	0	0	0	0	9	18	27
Aphididae	183	0	183	47	1	48	4	0	4	0	0	0	0	0	0	1	0	1
Cercopidae	1	3	4	1	1	2	0	0	0	0	0	0	0	0	0	0	1	1
Cicadellidae	284	53	337	138	2	140	6	10	16	0	0	0	0	0	0	8	16	24
Cixiidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Delphacidae	1	0	1	4	0	4	0	0	0	0	0	0	0	0	0	0	1	1
Fulgoridae	48	19	67	12	3	15	0	0	0	0	0	0	0	0	0	0	0	0
Membracidae	22	15	37	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	49	1	50	0	0	0	0	0	0	1	0	1	2	0	2	4	0	4
Apidae	39	1	40	0	0	0	0	0	0	1	0	1	2	0	2	4	0	4
Braconidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chalcidoididae	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dryinidae	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Number of Individuals

Table 19d.

Order / Family	Number of Individuals																	
	Sweep Method									Box Method								
	Forbs			Grass			Wheat			Forbs			Grass			Wheat		
	A	I	T	A	I	T	A	I	T	A	I	T	A	I	T	A	I	T
Hymenoptera (cont.)																		
Formicidae	23	0	23	4	0	4	0	0	0	1	0	1	1	0	1	2	0	2
Halictidae	4	0	4	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Ichneumonidae	5	0	5	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1
Pompilidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphecidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphiidae	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vespidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
misc.	4	1	5	2	0	2	0	0	0	0	0	0	0	0	0	1	0	1
Lepidoptera	13	60	73	5	22	27	0	5	5	0	4	4	1	2	3	0	0	0
Eucleidae	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0
Geometridae	0	2	2	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0
moth (misc.)	9	0	9	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Noctuidae	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
misc.	4	56	60	0	18	18	0	5	5	0	2	2	1	2	3	0	0	0
Neuroptera	12	6	18	0	0	0	2	0	2	0	0	0	1	0	1	0	0	0
Chrysopidae	8	1	9	0	0	0	2	0	2	0	0	0	1	0	1	0	0	0
Coniopterygidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemerobiidae	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
misc.	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coenagrionidae	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 19e.

Number of Individuals

Order / Family	Sweep Method Forbs A	I	T	Sweep Method Grass A	I	T	Sweep Method Wheat A	I	T	Box Method Forbs A	I	T	Box Method Grass A	I	T	Box Method Wheat A	I	T
Orthoptera																		
Acrididae	20	619	639	62	402	464	3	15	18	0	1	1	1	22	23	0	2	2
Gryllidae	4	467	471	53	364	417	3	15	18	0	0	0	0	13	13	0	1	1
Phasmatidae	9	56	65	0	0	0	0	0	0	0	1	1	1	3	4	0	1	1
Tettigoniidae	1	0	1	2	0	2	0	0	0	0	0	0	0	6	6	0	0	0
misc.	6	95	101	7	38	45	0	0	0	0	0	0	0	0	0	0	0	0
Psocoptera																		
Pseudocaeciliidae	0	1	1	2	0	2	33	0	33	0	0	0	0	0	0	2	1	3
misc.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thysanura																		
misc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichoptera																		
misc.	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Other Arthropods	155	0	155	61	0	61	15	0	15	1	0	1	12	0	12	16	2	18
house centipedes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
pill bugs	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0
spiders	154	0	154	61	0	61	15	0	15	1	0	1	9	0	9	16	0	16
ticks	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

1 The following notation is used: A - adult; I - immature; T - total.

A TIME BUDGET OF THE MALE DICKCISSEL (SPIZA AMERICANA)

by

ROBERT LEIGH SCHARTZ

B. S., Kansas State University, 1966

———————————————

AN ABSTRACT OF A MASTER'S THESIS

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Manhattan, Kansas

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An average time budget, compiled from 326 hours of field observations during the summers of 1966, 1967 and 1968, was constructed for the diurnal and reproductive cycles of the male Dickcissel (Spiza americana). Foraging varied less than any other activity, changing little from day to day and lacking a typical bimodal diurnal pattern. This was explained on the basis that energy demands paralleled the sustained level of activity characteristic of polygynous behavior and that energy demands of thermoregulation did not change since temperatures were seldom below 60° F. Males foraged with females, particularly during the courtship period, enabling them to meet their own energy demands while maintaining the pair bond. High levels of resting in the afternoons of 1966 corresponded inversely with reduced time spent singing. For temperatures greater than 94° F in 1966 resting increased and increased at a greater rate with increases in relative humidity. It was suggested that a significantly higher level of resting due to physiological heat stress resulted in a compensatory shift in the time budget leading to early cessation of breeding activities in 1966. Temperatures in 1967 did not exceed 94° F and resting did not change. Singing was highest early in the breeding season and in the mornings when courtship activities were more intense but male Dickcissels sing constantly throughout the day and singing normally averaged at least 50 percent of the time budget. Territory defense was highest at the time of territory establishment. Courtship gradually increased with the arrival of females and a peak occurred in the week prior to the height of nesting. Maintenance of the female during the reproductive season corresponded with the nesting activity and no diurnal pattern was evident. Interspecific aggression was seldom observed. It was hypothesized that in 1967 male Dickcissles left their territories (distant flight) to assess the population

density and habitat suitability in other locations. Singing was suggested to be an epidiectic display used as a cue by the birds to assess population densities. In a multiple regression analysis the number of mates was assumed to be an index of the suitability of the habitat a male occupies. The results were significant and showed that for fewer mates distant flight increases. Distant flight decreased from day to day and increased with time of day. A significant inverse correlation between the mean time spent foraging and the mean time spent in distant flight was consistent with the hypothesis since foraging behavior may be used to assess the desirability of a habitat. In 1966 increased water requirements may have resulted in a higher incidence of distant flight since open water is rarely available on the territory.

Means of territory sizes of males in 1967 were not significantly correlated with the mean number of mates or the total number of nests constructed on the territory. Differences in territory sizes in 1967 were not attributable to time spent in any activity but rather to differences in vegetation development. A lower density of males and fewer mates per male was indicative of a lower habitat suitability in 1966 as compared to 1967. The level of activity of the males was positively correlated with the number of mates present on the territory and no significant correlation was detected between the average number of mates per male and time spent singing.